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SPINNER, AN INHERITED TYPE OF ABNORMAL BEHAVIOR IN THE BEACH MOUSE, PEROMYSCUS POLIONOTUS

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INTRODUCTION

THE occurrence of "waltzing" in a stock of Peromyscus polionotus rhoadsi was reported by Watson (1939), who stated that this character seems to have single recessive inheritance. At the time of her report the case for the fact and for the mode of inheritance of this type of behavior in the rhoadsi stock rested upon the segregation of affected and unaffected animals in one sibship of sixteen mice produced by related normal parents. It seems worth while, therefore, to put on record the results of a considerable number of subsequent matings made at the Laboratory of Vertebrate Biology. The additional data here presented do not change the original conclusion, but provide it with a more substantial basis of fact. A detailed description also is given of the abnormalities of behavior exhibited by affected animals.

In the genus Peromyscus the term "waltzer" has been hitherto applied to a mouse of any strain which turns around briskly and repeatedly in a horizontal plane (Sumner, 1932: 39; Dice, 1935; Watson, 1939). Two genetically distinct types of "waltzing" are known in the species P. maniculatus (Dice, 1935; Watson, 1939). This report presents evidence that the phenotypically similar character which was discovered in a stock of P. p. rhoadsi constitutes a third genetic entity.

In order to avoid possible confusion among separate genetic characters which phenotypically appear somewhat alike, the designation "waltzer" is here restricted in the genus Peromyscus to mice whose genes for turning in small circles came originally from a stock of P. m. bairdi from Alexander, Franklin County, Iowa, trapped by Paul A. Moody in 1926 (Dice, 1935; Watson, 1939). The execution of rapid turns in tight circles in a horizontal plane will be called by the general term "whirling." This term was used by Yerkes (1907: 32) to describe a similar type of behavior in the house mouse (Mus musculus). The strain of mice which is characterized by whirling and sound-induced convulsions, and whose genes for abnormal behavior are derived from a stock of P. m. artemisiae from Lyons Ferry, Franklin County, Washington, collected by L. R. Dice in 1928 (Dice, 1935; Watson, 1939), will be called the "EP strain." The name "spinner" is here proposed for the behavior abnormality which originated in the rhoadsi stock and which previously has been reported as "waltzing" (Watson, 1939).

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BREEDING STOCKS

All the mice used in this study were laboratory bred. Information concerning the heredity of the spinner character was obtained from the F_1, F_2, and backcross generations of outcrosses of spinners to mice of the species polionotus which lacked any whirling tendencies and from matings among spinners which were extracted following these outcrosses. Three successive outcrosses were made:

Outcross I. — A male spinner from a stock of P. p. rhoadsi was mated to a female nonspinner from a stock of P. p. albifrons. The spinner was one which had been observed by Watson (1939). It came from a brother-sister mating and belonged to the second cage-bred generation of a stock of mice collected at Leesburg, Lake County, Florida, by C. C. Goff in 1934. It is highly probable that one of its two field-caught grandparents carried a gene for spinner. The nonspinner was a descendant of mice from Round Lake, Jackson County, Florida, and from Seminole Hills near Westbay, Walton County, Florida, collected by Don Hayne in 1935.

Outcross II. — Two female spinners of the F_2 generation of outcross I were mated to two nonspinners of a stock of hybrids between P. p. albifrons and P. p. leucocephalus. The nonspinners were descendants of P. p. albifrons from Crystal Lake, Washington County, Florida, and of P. p. leucocephalus from the south side of Santa Rosa Island, 2.5 miles east of Fort Walton Bridge, Escambia County, Florida, collected by Don Hayne in 1935.

Outcross III. — One female and two male spinners obtained from matings among spinners extracted following outcrosses I and II were mated to one male and two female nonspinners, respectively, from a stock of P. p. leucocephalus. The nonspinners were descendants of mice from Santa Rosa Island, opposite Camp Navarre, Santa Rosa County, Florida, collected by W. Frank Blair in 1942.

To test the genetic identity of spinner with waltzer and with whirling in the EP strain, recessive characters in the species P. maniculatus which are phenotypically similar to spinner, interspecific crosses were made. As noted above, the gene for waltzer came from a stock of P. m. bairdi from Alexander, Iowa, and that for whirling in the EP strain from a stock of P. m. artemisiae from Lyons Ferry, Washington (Dice, 1935; Watson, 1939). Both the waltzers and the whirlers from the EP strain which were mated to spinners, however, were hybrids between a number of different subspecies of P. maniculatus. The productive crosses were as follows:

Two male spinners extracted in the F_2 generation of outcross I were mated with two female waltzers.

Three matings involved two male spinners extracted following outcross III and three females of the EP strain which both whirled and had sound-induced convulsions.

METHOD OF TESTING

To identify a mouse as a spinner or a nonspinner it was placed in an examination box and watched for 90 seconds. Three different boxes have been used for observing the behavior of the mice. One was open-topped with galvanized metal walls, one was open-topped with wooden walls and floor, and one was a closed wooden box with a glass window in the cover. All three boxes were of approximately the same dimensions. The one most recently employed was 35.5 by 24 by 18 inches high. Transfer of the animal to the examination box was made by seizing the base of the tail with rubber-tipped 12-inch thumb forceps. During many of the trials keys were jingled throughout the 90-second period. Key jingling was not employed, however, during some of the more recent trials because this stimulus seemed to have little value for inducing whirling in these animals. If, without a sound stimulus, the mouse remained inactive, it was gently prodded with the forceps. After the 90-second period of observation, the mouse was caught and returned to its cage. Occasionally, a mouse which had appeared normal in the box earlier would whirl during the chase which preceded its capture.

During the observation period a spinner usually exhibited various grades of whirling. In order to record the amount and vigor of the abnormal behavior a grading system was employed which was based on the number of consecutive turns made without stopping and on the rapidity of turning. Five grades were defined as follows:

Grade N— Either the behavior seemed normal or the mouse ran in a zigzag path or in figure eights, but did not whirl through 360°.

Grade A— The mouse whirled through 360°, but a rest or some other form of activity intervened before another similar whirl was made.

Grade B— At least two small circles were turned in quick succession with no apparent stop between turns.

Grade C— The mouse turned many tight circles before stopping. The outline of the mouse was somewhat blurred.

Grade D— The mouse turned so rapidly that its outline was very much blurred.

The grade of performance recorded for each trial was the highest grade exhibited during the trial period. In general, the mice which turned the greater number of circles before stopping devoted a larger proportion of time to whirling than did those mice which made fewer consecutive turns. The number of turns executed during the 90-second period, therefore, on the average was higher for each successive grade from N to D.

Any mouse which did not whirl through at least 360° on the first trial was tested again on a later day. If it failed to whirl on the second trial, it was tested a third time. A mouse which whirled through 360° or more during any 90-second period of observation or during the subsequent attempt to catch it, was recorded as a spinner. Tests were repeated on some but not on all of the mice which were identified as spinners on the first or second trial. A mouse which consistently failed to whirl on all three trials was classified as a nonspinner. A few mice which appeared normal in the tests given them were lost before they had had three trials. These mice also were included in the nonspinner class.

Turning in figure eights and running in a strongly zigzag path are patterns of behavior which were commonly observed, but they were not recorded for every trial on which they were displayed. They have the appearance of being weak manifestations of a whirling tendency. Every mouse which was recorded as having exhibited either of these patterns of turning on any test was also seen to whirl either on the same or another trial and was accordingly classified as a spinner. The nonspinner class includes no mice credited with any whirling tendencies whatever, but it may contain a few that exhibited weak symptoms which were not recorded.

The first trial usually was made when the mouse was about a month old, but ages of mice at the time of the first routine test ranged from 23 to 137 days. Intervals between trials for most of the mice were about a month, but four mice of the F_1 generation of the cross between a spinner and a whirling convulsive of the EP strain were tested at intervals of from four to six days. These four mice were 47 days old when they were last tested. Ages of others at the time of their third trial varied from 82 to 211 days.

An indication of the effectiveness of three tests for discriminating between spinners and nonspinners is provided by the distribution of identifications of spinners among the first, second, and third tests. Only spinner offspring are expected from matings of spinner x spinner. Among a total of 111 mice produced by such matings 108 whirled on the first test, two others whirled on the second trial, and one which failed to whirl when it was first watched was lost before the time scheduled for it to be observed again. In the F_2 and backcross generations from crosses of spinner x unrelated mice which lacked whirling tendencies, 91 mice whirled on the first trial, eight others were identified as spinners on the second trial, and one additional mouse on the third trial. Inasmuch as all but one of the mice which were seen to whirl were observed to do so before the third trial, three tests at monthly intervals are concluded to have been enough to elicit whirling in a very high proportion of the mice which would ever have whirled under the conditions of testing. Even those identifications of nonspinners which, because of early loss of the mice, were based on a single test would seem to have a fair degree of accuracy.

DESCRIPTION

Spinners, like waltzers and like whirlers of the EP strain (Dice, 1935; Watson, 1939), whirl both clockwise and counterclockwise. Some individuals seem to whirl equally well in both directions; others exhibit a higher grade of whirling in one direction than in the other.

In order to analyze the motion of the feet during whirling, slow-motion pictures (64 frames per second) of a spinner were taken from directly beneath through a glass plate (Figs. 1-32). The rate of whirling is about two turns per second in the sequence illustrated. At times, however, spinners have made more than four revolutions per second.

When a spinner whirls, the hind leg of one side usually moves in unison with the front leg of the opposite side and alternately with the front leg of the same side and with the opposite hind leg. The position in which the feet of one side are close together and those of the opposite side are far apart (Figs. 10, 18, 25) commonly recurs.

Each front foot in turn is set down beneath the head (Figs. 10, 17, 23) and then pushes back diagonally toward the outside of the circle until the leg is fully extended. At the end of its thrust the front leg on the outer side of the circle stretches caudad and to the side of the mouse, usually forming a pronounced angle with the body (Figs. 1 and 17), but sometimes lying close to the side (Fig. 31). The front leg on the inside of the circle, at the conclusion of its step, lies beneath the mouse with the foot at or beyond the mid-line (Figs. 9 and 25).

The hind feet, working alternately, push straight back. The steps of the hind foot on the outer side of the circle are long and usually end with the leg completely extended (Fig. 25). The steps of the hind foot on the inner side of the circle are short, and the leg on this side usually is not greatly extended at the end of its step (Figs. 2 and 19).

While the mouse is whirling, the front part of its body is bent in the direction of the revolution. The curvature becomes most pronounced during the diagonal thrust of the outer front foot. With the strong backward shove of the outer hind foot the hind quarters next approach alignment with the front quarters. The whirling proceeds with alternate bending and partial straightening of the body. During the entire turn the tail bends inward and forward toward the nose, which also is directed inwards. The tail is most strongly curved when the body of the mouse is most sharply bent. At times the nose and tail overlap.

During the whirl none of the feet is used as a pivot, but all feet take recurrent short or long steps. Usually the outside hind foot takes much longer steps than the inside foot. Fairly long steps are taken by both front feet.

Whirling is the most spectacular feature of a spinner's behavior. Sometimes, however, spinners run in large circles, in figure eights, or in a zigzag or sinuous path, and sometimes their course appears normal.

Watson (1939), who had only a few spinners to observe, stated that they showed no nervous head movements. The vigorous sidewise jerks of the head made while the nose points forward and the mouse stands still or backs, which are seen in waltzers and in whirlers and convulsives of the EP strain, have not been observed in spinners. Less vigorous head shaking, however, both in the horizontal and in the vertical plane have been noted in most spinners which are now in the laboratory, although the movements are not equally pronounced in all spinners. The shaking is sometimes rapid, when it seems clearly to constitute a tremor. When its rate is slower, it often resembles the sniffing motions of a normal mouse. The tremor usually is restricted to the head, but a few spinners more than six months old have exhibited violent rocking from side to side of the entire body.

The sidewise movements of the head in spinners usually are of slight magnitude. The head is often tossed upward, however, until it is tilted at a pronounced angle, and it is sometimes held in this position for an appreciable length of time. While walking, some spinners carry the head higher than normal mice usually do. The sharpest upward tilts of the head, however, are made while the spinner is standing still or sitting. One or both forepaws are sometimes lifted as the mouse points its nose upward. This peculiar head carriage has not been noted in all spinners, nor have all those spinners which have displayed it done so every time that they were watched. Of 17 spinners which were checked three times each especially for head tilting, six demonstrated the peculiarity each time, two displayed it on only two of the trials, six exhibited it only once, and three did not show it on any trial. Thirty-eight nonspinners which had spinner parents or sibs were checked once for abnormal head movements. No excessive tilting or shaking of the head was seen in any of these nonspinners. Nervous head movements, including upward tilting of the head, together with whirling form part of the snydrome of a number of genetically distinct characters in the house mouse (Yerkes, 1907: 31, and frontis.; Grüneberg, 1952, see especially Fig. 26, p. 187).

Watson (1939) reported that whirlers and convulsives of the EP strain become deaf at a mean age of 6.8 ± 0.5 months, and that 16 months is the oldest age at which an affected mouse of this strain has been able to hear. She noted that waltzers keep their hearing ability for a longer time, but that these mice also become deaf when they are from 18 to 27 months old. In a number of inherited behavior abnormalities in the genus Mus, also, deafness accompanies whirling behavior (Grüneberg, 1952: 178-96). Spinners as young as 19 days are less responsive than related nonspinners to a squeak made by pressing the lips against the upper teeth and inspiring through the mouth. Fifty-six nonspinners, aged 19 days to 27 months, which were close relatives of spinners, all responded to this stimulus with a pronounced ear movement or a jump. Of 55 spinners which were exposed to this sound, two, aged 27 and 56 days, moved their ears slightly in response to it, and 53, aged 19 days to 26 months, showed no visible reaction to it.

Not all these spinners, however, were completely deaf. The sound made by tapping a glass tumbler with metal forceps, which was the stimulus used by Watson (1939) to test hearing ability, induced jumps in many of the same mice which had failed to respond to the squeak. Of 32 spinners, aged 6 to 20 months, 28 reacted to the ring of forceps on glass either with a movement of the ears or with a jerk of the head or body, and of 18 spinners aged 21 to 28 months, 6 responded to this sound. The difference between the two age classes in responsiveness strongly suggests that the hearing of spinners becomes progressively worse with advancing age.

Some loss of hearing probably takes place in nonspinners also as they become old. One mouse which was heterozygous for the spinner character had reacted strongly to a vocal squeak when it was 27 months old, but at 37 months it gave only a slight flick of its ears in response to a squeak, although it still reacted definitely to the sound of forceps striking glass. Although this nonspinner evidenced some loss of hearing it seemed to hear as well at 37 months as any of the young spinners. Between the ages of 19 days and 27 months no case of overlapping of hearing acuity of spinners and nonspinners was found. Tests have not been made with pure tones to ascertain the range of frequencies to which spinners and nonspinners will respond.

Inability to swim on the surface of water is one of the characteristics of several inherited abnormalities of behavior in the genus Mus (Grüneberg, 1952: 178-97). The swimming ability of 21 spinners was tested by placing them in a pan of water. None of them stayed on the surface for more than a few strokes, and all but six went under the surface immediately. While their heads were above water some of the six swam in straight lines, others swam in circles. Under water the spinners swam in an erratic course with constant twisting and turning which was not restricted to any one plane. They not only described circles in a horizontal plane but rolled over repeatedly and also turned backward somersaults. These animals would have drowned if they had not been quickly rescued. Ten nonspinners which were, however, relatives of spinners, swam without difficulty on the surface of the water. They usually proceeded in a straight line from the spot at which they were dropped to the side of the pan of water and then swam repeatedly around the pool staying close to its side.

Stimuli which have proved effective for inducing whirling in a number of strains of Peromyscus include the placing of the mice in a strange cage, the jingling of keys, or a pinch on the tail (Dice, 1935). Spinners whirl with little or no stimulation (Watson, 1939). In this study, however, identification of mice as spinners or nonspinners was made immediately after they were transferred from their cage to a box. They therefore always received both the stimulus of an unknown environment and that of being handled, and during many of the tests keys were jingled also.

To measure the efficiency of key jingling as a stimulus to induce whirling in spinners, 14 mice which had been identified as spinners and 24 related mice which had been identified as nonspinners were placed one at a time in the observation box and watched first without key jingling and then with it. All 24 nonspinners were inactive while the keys jingled. Each of the 14 spinners whirled before the keys jingled, but one of them failed to whirl during jingling. Of the other 13 spinners, one was less active during jingling than it had been earlier, two showed an increase in activity when jingling began, followed by a decrease to a level lower than that exhibited without jingling, and ten were equally active with and without jingling. The fact that key jingling elicited very little change in the activity of spinners may be a consequence of their defective hearing.

VARIABILITY

Observations of behavior were made primarily for the purpose of distinguishing between spinners and nonspinners rather than to measure the variability of performance of spinners. The grading is not believed to have been sufficiently consistent to provide a fully reliable measure of variability. Standard tests of heterogeneity, therefore, are not presented. For descriptive purposes, however, the grades assigned are believed to provide a better indication of the vigor of whirling exhibited than could be given without a grading system. Many of the observations throughout the course of the study were made by me, and from time to time I checked the grading of each of the assistant observers. Differences of opinion as to grade of whirling were noted only when the performance seemed close to the border line between two grades. Inconsistencies in grading, therefore, are believed to be largely restricted to performances differing by less than one unit on the grading scale.

In order to be able to calculate means of grades, numerical values from 0 to 4 were assigned to the grades N, A, B, C, and D, respectively. Means and their standard errors were calculated on the assumption that the five successive grades represent mid-points of five equal subdivisions on a scale extending from -.5 to 4.5.

The grade of whirling exhibited by a particular mouse varies from moment to moment. The highest grade of performance during a 90-second period of observation also varies from test to test of the same mouse. Recorded fluctuations from test to test greater than those between two adjacent grades almost certainly indicate differences in vigor of whirling at the separate times. Changes of this magnitude from test to test were observed in 19 of 74 spinners which were tested three times each.

Whirling has been observed in spinners as young as 17 days and as old as 31 months. Within the age limits at which spinners were regularly tested, from 23 to 211 days, no pronounced change in grade of whirling with age has been noted. Whether any of the variability from test to test is attributable to age is not certain. Fifty-three spinners which were given their first test when they were less than 53 days old were each tested two more times at monthly intervals. Increases in grade of whirling with advancing age were noted among these spinners more often than decreases. The mean grades for the three successive tests are 1.6 ± .1, 1.9 ± .1, and 2.1 ± .1, respectively. These spinners, however, do not constitute a random sample. Because the group includes a disproportionately high number of spinners which failed to whirl on the first trial, its mean grade of whirling on the initial test is low. The apparent effect of age on grade, therefore, may be a statistical artifact resulting from the selection of the mice to be retested.

From matings of spinner × spinner 111 mice were produced, all of which were expected to be spinners. One hundred other mice were identified as spinners in the F_2 and backcross generations derived from outcrosses of spinners to mice which lacked whirling tendencies. Grades of whirling were recorded for 208 of these 211 spinners. The mean of the grades on the first trial are 1.9 ± .1 for 82 spinners of outcross group I, 2.3 ± .1 for 50 spinners of outcross group II, and 1.7 ± .1 for 76 spinners of outcross group III. Three other spinners, two of outcross group I and one of outcross group III, whirled on the first test, but their grade of performance was not recorded.

Within the outcross groups the mean grades of whirling for the sexes are: group I, 1.9 ± .1 for 39 females and 1.8 ± .1 for 43 males; group II, 2.2 ± .2 for 22 females and 2.3 ± .2 for 28 males; and group III, 1.7 ± .1 for 52 females and 1.7 ± .2 for 24 males. The differences in grade between the sexes are small and are not consistent in direction. There is, therefore, no indication that sex influences grade of whirling among spinners.

It seems highly probable that individual differences in grade of whirling exist. The mean grade of whirling exhibited by the 74 spinners which were tested three times each is 2.0 ± .1. Eight of these spinners, however, failed to exhibit whirling of a grade higher than A on any test. Six of them, on the other hand, gave performances of grade C or higher on each test. A further indication that differences in grade exist among spinners lies in the fact that attempted demonstrations of whirling by spinners have been more often successful when the spinners exhibited were selected on the basis of a previous record of a high grade of whirling than when they were picked at random.

HEREDITY

The distribution of spinners and nonspinners in the F_1, F_2, and backcross generations and among offspring from matings of spinner × spinner is given in Table I.

The F_1 generation derived from outcrosses of spinners to nonspinners of other races of the species polionotus consisted of 50 mice distributed

TABLE I

Frequency Distribution of Nonspinners and Spinners, Males and Females, in Three Outcross Groups From Four Mating Types

Sp Sp = homozygous nonspinner; sp sp = spinner; Sp/sp = nonspinner from mating of nonspinner ♀ x spinner ♂; sp/Sp = nonspinner from mating of spinner ♀ x nonspinner ♂

Mating	Offspring																							
	Outcross Group I						Outcross Group II						Outcross Group III						Combined Outcross Groups					
♀ ♂	No. of sib-ships	Non-spin-ners		Spin-ners		Total	No. of sib-ships	Non-spin-ners		Spin-ners		Total	No. of sib-ships	Non-spin-ners		Spin-ners		Total	No. of sib-ships	Non-spin-ners		Spin-ners		Total
		♀	♂	♀	♂			♀	♂	♀	♂			♀	♂	♀	♂			♀	♂	♀	♂	
Sp Sp x sp sp	(1)	4	5	0	0	9							(2)	9	8	0	0	17	(3)	13	13	0	0	26
sp sp x Sp Sp							(2)	11	8	0	0	19	(1)	3	2	0	0	5	(3)	14	10	0	0	24
Total F_1	(1)	4	5	0	0	9	(2)	11	8	0	0	19	(3)	12	10	0	0	22	(6)	27	23	0	0	50
sp sp x sp sp	(6)	0	1	16	19	36	(4)	0	0	18	20	38	(4)	0	0	24	13	37	(14)	0	1	58	52	111
Sp/sp x Sp/sp	(2)	8	12	6	8	34							(6)	37	30	9	5	81	(8)	45	42	15	13	115
sp/Sp x sp/Sp													(2)	23	23	7	3	56	(2)	23	23	7	3	56
Total F_2	(2)	8	12	6	8	34							(8)	60	53	16	8	137	(10)	68	65	22	16	171
sp/Sp x sp sp													(4)	12	4	11	3	30	(4)	12	4	11	3	30
sp sp x Sp/sp	(2)	8	17	17	17	59							(1)	0	1	2	0	3	(3)	8	18	19	17	62
sp sp x sp/Sp							(1)	3	5	4	8	20							(1)	3	5	4	8	20
Total BC	(2)	8	17	17	17	59	(1)	3	5	4	8	20	(5)	12	5	13	3	33	(8)	23	27	34	28	112

among six sibships. The spinner parents of the F_1 generation were three females and three males which had exhibited whirling of grades A to C on the first trial. Four F_1 offspring were checked for whirling only twice. Each of the others was given at least three trials. Six of them were tested a fourth time when they were more than 300 days old. None of the F_1 offspring whirled on any trial.

Spinners which were extracted in the F_2, first backcross, and later generations of each outcross were mated among themselves. Fourteen such matings involving 14 female and 13 male spinners produced 111 offspring. Ten of the parents themselves came from matings of spinner x spinner. The others came from matings of nonspinner x spinner or nonspinner x nonspinner. The grades of whirling of the parents on the first trial were from N to C. Those which failed to whirl on the first trial whirled on the second trial. All but one of their 111 offspring whirled. The one apparent exception was a mouse which was tested only once. Inasmuch as failure to whirl on a single trial is known to be inadequate evidence on which to make an entirely reliable identification of nonspinner, the phenotype of this one mouse remains unknown.

Matings between spinners and mice of the F_1 generation of outcross groups I, II, and III produced a backcross generation which consisted of eight sibships with a total of 50 nonspinners and 62 spinners. Grades of performance of the spinner parents on the first trial were from A to C. One of the mice of the backcross generation which was classified as a nonspinner was given a single test. All others of this class were checked three times each. The observed distribution of nonspinners and spinners fits the expected 1:1 segregation well ($X^2 = 1.286$, with 1 degree of freedom), and no heterogeneity among outcross groups or among sibships could be demonstrated.

An F_2 generation was raised only in outcross groups I and III. In this generation an excess of spinners was observed in group I and a deficiency of spinners in group III. Heterogeneity between the two groups with respect to segregation in the F_2 generation is significant at the 1 per cent level (X^2, calculated from a 2 x 2 contingency table, = 8.821, with 1 degree of freedom). The results for each group consequently are presented separately.

Two sibships with a total of 20 nonspinners and 14 spinners comprised the F_2 generation of outcross group I. Each of the 20 nonspinners was tested three times. The lowest grade of whirling recorded for any of the spinners in these two sibships is B. Inasmuch as Grade B whirling is clearly distinguishable from normal behavior, the excess in the spinner class cannot be attributed to misclassification of offspring. The deviation from the expected 25.5 nonspinners and 8.5 spinners is significant at the 5 per cent level ($X^2 = 4.745$, with 1 degree of freedom).

Eight sibships with a total of 60 female and 53 male nonspinners and 16 female and eight male spinners constituted the F_2 generation of outcross group III. Three females and three males classified as nonspinners in this group were tested only once, and one female and one male were given only two trials each. The remainder of the nonspinners received three trials each. The deviation from the expected 102.75 nonspinners and 34.25 spinners is significant at the 5 per cent level ($\chi^2 = 4.090$, with 1 degree of freedom). When the sexes are considered separately the deviation from a 3:1 ratio is significant for males ($\chi^2 = 4.596$, with 1 degree of freedom) but not for females ($\chi^2 = 0.632$, with 1 degree of freedom).

The distribution of males in the three outcross groups roughly parallels that of spinners. In outcross groups I and II males slightly exceed females in number, and in the F_2 and backcross generations of these groups more than the expected number of spinners occur. Outcross group III has fewer males than females, and in the F_2 generation of this outcross group there is a deficiency of spinners. In outcross groups I and II the sex distribution of 95 females and 120 males does not deviate significantly from a 1:1 ratio ($\chi^2 = 2.907$, with 1 degree of freedom). In outcross group III the sex distribution is 84 females and 68 males among nonspinners, and 53 females and 24 males among spinners. The deviation from an expected 1:1 sex ratio is not significant in the nonspinner class ($\chi^2 = 1.684$, with 1 degree of freedom), but it is highly significant in the spinner class ($\chi^2 = 10.922$, with 1 degree of freedom). The sex distribution among nonspinners is significantly different from that among spinners in outcross group III (χ^2 for heterogeneity, calculated from a 2 × 2 contingency table, $= 3.915$, with 1 degree of freedom).

Whether the relationship observed between sex and spinners is more than a fortuitous one is not known. The disturbance of the sex ratio is significant only among spinners of outcross group III. The observed deviations from expectation are not such as would result from partial sex linkage of spinner. If spinner were a partially sex-linked character, a deficiency of male spinners and female nonspinners would be expected among offspring from matings in which the male parent was heterozygous for the spinner character and had received his single gene for spinner from his mother. The deficiency of male spinners in outcross group III, however, is not restricted to offspring from this mating type, and no deficiency of female nonspinners is observed among offspring from any mating type in this outcross group. Although it is clear that partial sex linkage by itself could not produce the observed pattern of disturbances in segregation, the absence of partial sex linkage is not proved. Because of the unexplained heterogeneity among outcross groups with respect to the single factor ratios for sex and spinner, the data are considered to be unsuitable for a rigorous test for partial sex linkage. The distribution of parental types and recombinations of spinner and sex in the F_2 and backcross generations, however, gives no indication of close linkage between these two characters.

If the deficiency of male spinners in outcross group III resulted from incomplete penetrance of the spinner character in males, an excess would be expected in the class of male nonspinners. No such excess in outcross group III occurs. Further evidence that low penetrance is not the cause of the deficiency of male spinners in outcross group III is the fact that with one exception offspring of both sexes from matings of spinner x spinner were seen to whirl. The one offspring of this mating type which failed to whirl on the single test given it belonged to outcross group I.

Conditions, either genetic or environmental, under which outcross group III was reared may have been such that male spinners were on the average less viable than other phenotypes. Such a hypothesis would explain the aberrant ratio of spinners and nonspinners in the F_2 generation of outcross group III. Failure to find a deficiency of spinners in the backcross generation of this outcross group may be related to the fact that it consisted largely of females. Unfortunately, records suitable for comparing the viability of the different classes were not made. The data available merely suggest that a future investigation of the relative mortality of spinners and nonspinners of each sex under different conditions might be profitable.

The absence of spinners in the F_1 generation, the expression of whirling in all mice adequately tested from every mating of spinner x spinner, and the distribution of spinners and nonspinners in the backcross generation demonstrate that spinner is a recessive character involving a single locus. Segregation in the F_2 generation, although disturbed, is not necessarily incompatible with the hypothesis that a single pair of recessive genes determines the spinner phenotype. No other pattern of inheritance fits the combined data. The results therefore support Watson's (1939) conclusion.

DISTINCTNESS FROM OTHER TYPES OF ABNORMAL BEHAVIOR

Waltzer is a recessive behavior abnormality whose principal manifestation is whirling (Dice, 1935; Watson, 1939). Mice of the EP strain have a recessive character the syndrome of which includes both whirling and sound-induced convulsions and which is genetically distinct from waltzer (Dice, 1935; Watson, 1939). The whirling exhibited by spinners closely resembles that of mice of the waltzer and EP strains. Such differences in behavior among these strains as have been observed might depend upon genes other than the ones which control whirling. Tests have therefore been made to ascertain whether the whirling of spinners is identical in heredity with the whirling exhibited by either of the other two strains.

Unless interaction between genes at separate loci permits whirling by double heterozygotes, no offspring from a mating between two different kinds of recessive whirling would be expected to whirl. In the F_2 generation from such a cross, if the heterozygotes display normal behavior, if whirling is exhibited by both single and double recessives, if penetrance is complete, and if the genes for the two kinds of whirling assort independently, the expected ratio of nonwhirlers to whirlers is 9:7. The expected proportion of whirlers would be less if penetrance were incomplete and slightly more if the genes for the two kinds of whirling were linked. From a mating between whirlers which are genetically identical the proportion of whirlers expected in the first and in subsequent generations is equal to the degree of penetrance of whirling.

In each of the three strains of whirling Peromyscus the penetrance of whirling has been observed to be high. From matings among spinners all offspring whirled which were adequately tested. From matings among waltzers Watson (1939) obtained 24 waltzers (89 per cent) among 27 offspring. In the EP strain whirling and convulsions were concluded by Watson (1939) to be manifestations of the same major gene. From matings among convulsive whirlers she obtained 43 offspring, all of which were either convulsives or whirlers or both.

Two matings between female waltzers and male spinners produced an F_1 generation of 14 mice. Both spinner parents and one of the waltzer parents gave a grade B performance on the first trial. The other waltzer parent appeared normal on the first test but whirled with a grade of B on the second trial. Each mouse of the F_1 generation was tested three times, but none whirled. The F_2 generation consisted of one sibship of 25 nonwhirlers and 12 whirlers. One of the nonwhirlers of this sibship was given only two tests. All of the other nonwhirlers were tested three times each. All but two of the whirlers performed on the first trial with grades of from A to C. Two mice were not identified as whirlers until the second trial. The distribution of nonwhirlers and whirlers in the F_2 generation does not differ significantly from a 9:7 ratio ($\chi^2 = 1.926$, with 1 degree of freedom). The composition of both the F_1 and F_2 generations, therefore, is in agreement with the hypothesis that spinner is a character genetically distinct from waltzer. Unless penetrance of whirling is less than 20 per cent in the F_1 generation and less than 49 per cent in the F_2 generation, the observed results differ significantly from those expected if whirling in the two strains is determined by the same pair of recessive genes. The test therefore gives strong preference for the hypothesis that spinner and waltzer are different characters.

Matings between three female whirling convulsives of the EP strain and two male spinners produced an F_1 generation of 11 mice. The two spinner parents whirled with grades of A and D, respectively, on the first test, and the three whirling convulsives with grades of C and D. Ten of the mice of the F_1 generation were tested three times each, and one was given a single test for whirling. None of these 11 mice whirled, and none showed convulsive behavior when keys were jingled. All of them responded with ear movement to a soft squeak. Their behavior was thus normal on all counts. The results are in complete agreement with the hypothesis that the gene for spinner is at a different locus from the gene for whirling in the EP strain. Unless penetrance in the F_1 generation is less than 24 per cent, the results are in disagreement with the hypothesis that the same pair of genes determines whirling in the two strains. Inasmuch as penetrance in both parental stocks has been observed to be much higher than 24 per cent, the results are interpreted as demonstrating that spinner is genetically distinct from the phenotypically similar character of the EP strain and thus constitutes a third type of inherited whirling.

This conclusion rests upon the assumption that penetrance in the hybrids is similar to that in the parental stocks. The crosses of spinners to whirlers of the waltzer and EP strains, however, were between different species. The hybrids, therefore, undoubtedly provided a genetic background somewhat different from that on which the genes for whirling operated in the parental stocks. That penetrance of whirling of the waltzer and EP strains is affected by genetic modifiers is indicated by the results of Dice (1935) and Watson (1939), who found deficiencies of whirlers following outcrosses of whirlers to other stocks. To what extent an interspecific cross would change the degree of penetrance of whirling is not known. The present information, nevertheless, gives strong support to the hypothesis that spinner is a third type of genetically determined whirling, and that mice doubly heterozygous for spinner and for either waltzing or for whirling of the EP strain have normal behavior.

The symbol sp is here proposed for the gene for spinner, and Sp for its normal allele.

SUMMARY

Spinner is an abnormality characterized by whirling, nervous head movements, deficient hearing, and inability to swim on the surface of water. It was first observed in the second cage-bred generation among offspring from a brother-sister mating in a stock of Peromyscus polionotus rhoadsi taken at Leesburg, Florida.

The vigor of whirling displayed by a given spinner varies from moment to moment, and at times a spinner appears to walk in a normal manner. Whirling, however, is exhibited frequently enough by spinners that they can be identified accurately by this peculiarity of behavior. Of 111 mice both of whose parents were spinners, 108 whirled during the first 90-second observation period. Of 100 other mice identified as spinners, 91 whirled the first time that they were watched.

Whirling has been observed in spinners as young as 17 days of age and as old as 31 months. Little or no effect of age on vigor of whirling has been noted in tests of spinners from 23 to 211 days old.

No difference between the sexes in vigor of whirling has been observed.

Recessive inheritance of the character spinner is demonstrated; thus support is given to Watson's statement (1939). Penetrance of the character among offspring from matings of spinner x spinner is high.

Evidence is presented that spinner is genetically distinct from waltzer and from the whirling that occurs in mice of the EP strain, both of which characters have been reported previously in Peromyscus.

The symbol sp is proposed for the gene for spinner.

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Figs. 1-32. Sequence of steps in one complete turn by a spinner viewed from below. Drawings of consecutive frames from motion pictures at 64 frames per second taken from beneath through a glass plate. 16-mm. film. Shutter speed 1/480 second.

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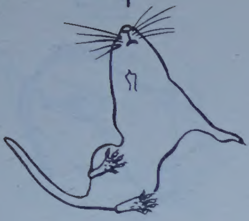

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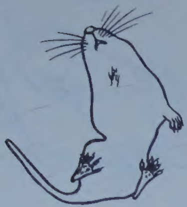

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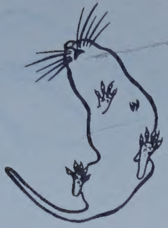

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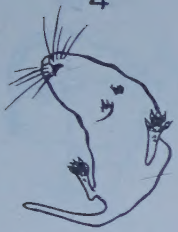

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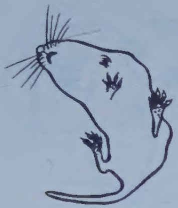

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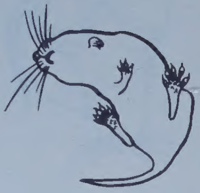

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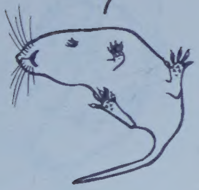

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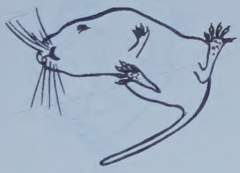

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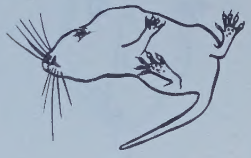

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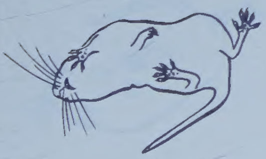

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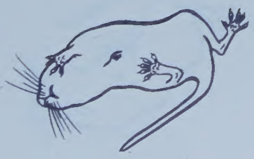

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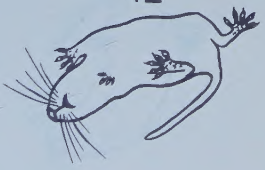

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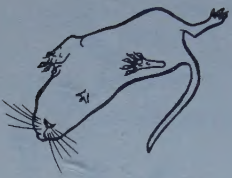

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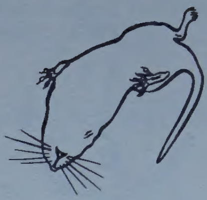

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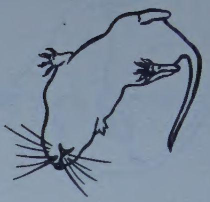

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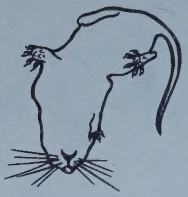

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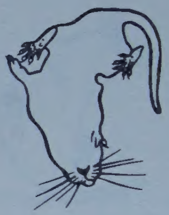

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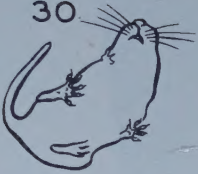

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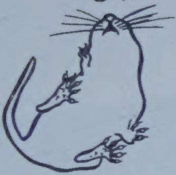

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